HYOBRANCHIAL APPARATUS OF THE CRYPTOBRANCHOIDEA (AMPHIBIA)

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ABSTRACT.—This report is a comparative study of the hyobranchial skeleton of the three species in the family Cryptobranchidae and four species of the family Hynobiidae, all of which are figured. Anatomical differences between the cryptobranchids and their relationship to hynobiids are noted and discussed. Reference is made to a relationship that may exist between these families and other salamander families, particularly the possible relationship of the Hynobiidae to the super families Ambystomatoidea or possibly Plethodontoidea.

The primary purpose of this study was to examine and compare the hyobranchial skeleton of representatives of the families Cryptobranchidae and Hynobiidae. We were concerned not only with the anatomical relationships of the two families, but also with the basic differences between available genera within the families. Much has been done to establish an understanding of anatomical relationships primarily involving skeletal and soft tissue comparative anatomy of other families, particularly Ambystomatidae, Plethodontidae, and Salamandridae. The studies by Humphry (1872) and Dunn (1923, 1926) were followed by research of Noble (1931), Francis (1934), Edgeworth (1935), Piatt (1935, 1939, 1940), Taylor (1944), Tanner (1950, 1952), Fox (1954), Wake (1966), Wake and Ozeti (1969), Nickerson and Mays (1972), Estes (1981), Duellman and Trueb (1986), and others cited below, involving cytogenetic studies with the intent to provide data showing familial relationships.

The examination of the relationships of the Cryptobranchoidea by Dunn (1923) established the primitive characters of external fertilization and retention of the angular bone in the lower jaw. These characters have not only placed the cryptobranchids and hynobiids as primitive groups of salamanders, but also as possible descendants of ancestral stock similar to those from which other salamander lines might have arisen. Dunn (1923) also noted the following: both families possess nasals that meet at the middorsal line, and the premaxillary spines are short in contrast to other families with separate nasals and long spines.

Recent studies also indicate that the cryptobranchids are primitive in that they have a large number of chromosomes (60). Morescalchi et al. (1977, 1979) give the structure and numbers of chromosomes for the three cryptobranchid species, with each having 60, and list the following hynobiid species and their chromosome numbers: *Ranodon sibiricus*, 2n = 66; *Batrachuperus mustersi*, 2n = 62; *Onychodactylus japonicus*, 2n = 58 ± 2; *Hynobius dunni*, *H. nebulosus*, and *H. tsuensis*, each with 2n = 56. A study by Sessions et al. (1982) provides essentially the same information, listing 30 pairs of chromosomes in the genus *Andrias* as compared to 11–14 pairs in other families of North American salamanders. Taketa and Nickerson (1973) determined the relative electrophoretic mobilities of the hemoglobins of three families of salamanders represented by *Cryptobranchus*, *Necturus*, and *Hynobius*, when compared with adult human HbA, at pH 8.4. It is noteworthy that *Cryptobranchus* has a single component with greater mobility than the two components in *Hynobius tsuensis*.

The relationship of the cryptobranchids to other families of salamanders and particularly to the hynobiids was noted by Dunn (1923). He indicated that cryptobranchids are more closely related to the hynobiids than perhaps to other salamander families. While this may yet be true, there are substantial differences between the basic structures of the throat anatomy of the hynobiids and the cryptobranchids. This is particularly evident in the bony and cartilaginous structures. If there is indeed a close relationship, it is apparently one based on such characters as external

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fertilization, retention of the angular bone, and greater number of chromosomes, and not on the hyobranchial structures, which have undergone major modifications that would suggest not only an extended period of isolation, but certainly one in which major adaptive modifications have occurred. Furthermore, there has been a major radiation in the family Hynobiidae that has not occurred among the cryptobranchids.

The fossil history of the development of the various families of salamanders indicates that there may have been a movement of representatives of two major families from North America into the Orient. Certainly North America has been a center for major salamander evolution, with all families (except Hynobiidae) being represented. Only four of the seven families have extended their distributions beyond the North American shores (Plethodontidae—Europe; Ambystomatidae, Cryptobranchidae, and Hynobiidae—Asia). The families Ambystomatidae and Cryptobranchidae are represented on both the Asiatic and American continents, with the Asiatic cryptobranchids having developed giantism and undergone a more complete morphological development than the American representatives.

The place of origin for the Cryptobranchoidea and particularly the family Cryptobranchidae is as yet uncertain. Meszoely (1967) described as new the genus *Piceoerpeton* from fossil vertebrae obtained from the early Eocene of Wyoming and included it in the family Cryptobranchidae. Within the family it is related to the genus *Andrias*. Estes (1969) maintained that the relationship of the genus *Piceoerpeton* is better placed in the family *Scapherpetontidae*, a representative of Ambystomatoidea. The occurrence of *Andrias* in Europe and Japan (Westphal 1958) suggests a previously wide distribution for the family and perhaps for the genus *Andrias* in North America, although this has not as yet been demonstrated.

An examination of the throat skeleton suggests that *Andrias* has advanced beyond the semilarval condition seen in *Cryptobranchus* with its retained gill bars (Figs. 1–3). The two oriental species (*A. davidianus* and *M. japonicus*) have a greater similarity in hyobranchial structures than either has with adult *C. alleganiensis*, and both are much larger.

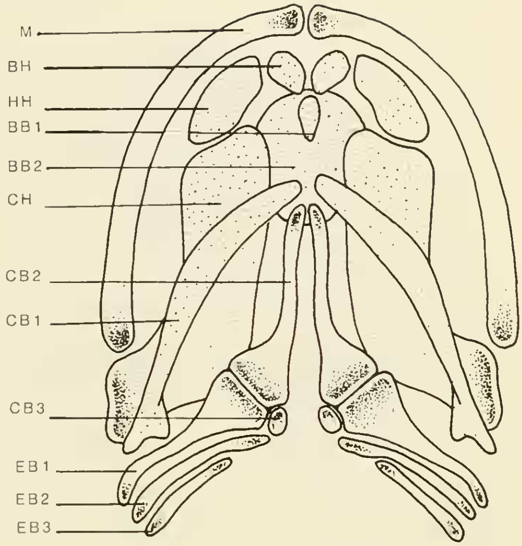

Fig. 1. Ventral view of the hyobranchial apparatus of *Cryptobranchus alleganiensis*. M = lower jaw; BH = basihyal; HH = hypohyal; BB1 = basibranchial #1; BB2 = basibranchial #2; CH = ceratohyal; CB1 = ceratobranchial #1; CB2 = ceratobranchial #2; EB1 = epibranchial #1; BB3 = basibranchial #3; EB2 = epibranchial #2; EB3 = epibranchial #3.

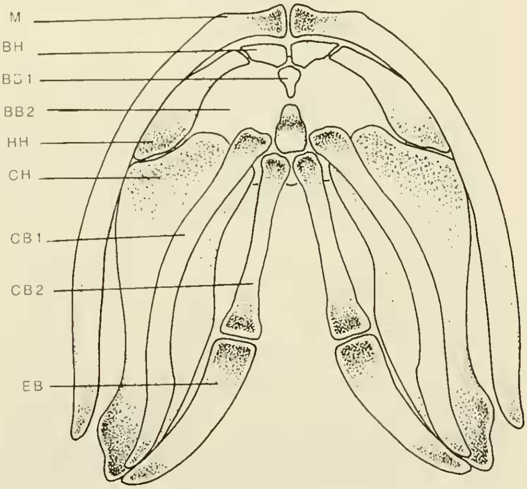

Fig. 2. Ventral view of the hyobranchial apparatus of *Megalobatrachus japonicus*.

A comparison of the hyobranchial skeleton of Hynobiidae to that of Cryptobranchidae indicates major differences not only in the position of basic structures but also in relative size and shape (Fig. 4). If these families are retained in the same superfamily (Cryptobranchoidea), their retention must be based

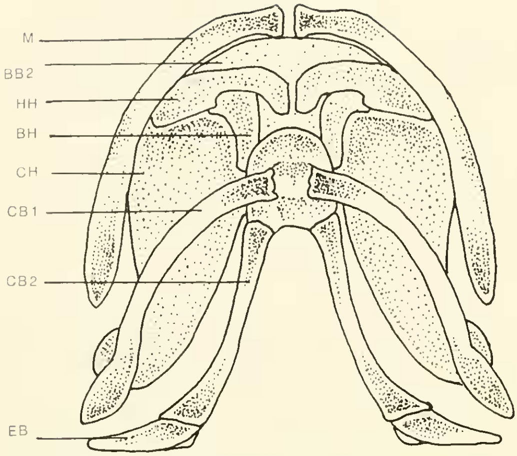

Fig. 3. Ventral view of the hyobranchial apparatus of *Andrias davidianus*.

on the primitive characters indicated above and not on the skeletal characters of the throat.

The following is a description of the structures of the hyobranchial apparatus as observed in some members of the superfamily Cryptobranchoidea.

The hyobranchial apparatus of the family Cryptobranchidae consists of cartilaginous and bony elements. It has the following features: basibranchials, ceratohyals, hypohyals, basihyals, ceratobranchials, and epibranchials. The first basibranchial is a small cartilage located in the anterior median area of the throat. It is loosely joined to the basihyals and is ventral to the enlarged second basibranchial. It was observed in all dissections except *Andrias davidianus*. The second basibranchial is larger than the first and is platelike in all. It provides broad support for the floor of the mouth, joins with the first and second ceratobranchials and in the Asian species includes a distinct ventral process that makes a strong joint with the ceratobranchials. This cartilage is largest in the Asian species, filling the anterior third of the space between the rami of the mandibles. The basihyals, hypohyals, and ceratohyals form a cartilaginous arch that follows the contour of the jaw. There does not appear to be any hard tissue connection between the elements of this arch and other hyobranchial structures. *Andrias davidianus* differs from all others in the arrangement of the basihyals and the hypohyals. The hypohyals are enlarged and curved, meeting at the midventral line and also forming a broad joint with the ceratohyals. The basihyals have been pushed caudad and lie on the medial border of the ceratohyals and the posterior border of the hypohyal. There is some doubt as to the proper names to be applied to these cartilages; a final determination may require a careful examination of the embryonic development of these structures in this species.

An examination of the position of the hyobranchial apparatus in the two families (Figs. 1–4) indicates a noticeable posterior shift of all structures in the family Hynobiidae. This has raised a question as to whether the structure we have labeled the first basibranchial in Figures 1 and 2 is a basibranchial or a separate segment of the first arch. In any case it is not possible to relate these structures (basibranchials) to homologous structures in hynobiids using only adult specimens.

The structure of the hyobranchial apparatus has been illustrated as we found it to occur in the dissections of *Andrias davidianus*, *Megalobatrachus japonicus*, and *Cryptobranchus alleganiensis* (Figs. 1–3). The semilarval condition of the American hellbender (*C. alleganiensis*) is evident by the presence of gill bars, which are ossified, and by the remaining gill slit (Fig. 3). These structures were found in both *C. a. alleganiensis* and *C. a. bishopi*. No such structures were found in the Asian species. Both ceratobranchials were ossified in the Asian forms, but in *Cryptobranchus* only the second ceratobranchial shows evidence of ossification. The cartilage components of *Cryptobranchus* are rounded and tend to be loosely joined; this condition also suggests the immature status of the American species.

The hyobranchial apparatus of *Hynobiidae* was determined by dissection of four species: *Hynobius naevius*, *H. keyserlingii*, *H. tsuensis*, and *Ranodon sibiricus*. The hynobiid salamanders show remarkable conformity to a specific morphologic pattern that is unlike that found in any other salamander group. The curious structure of the ceratohyals is an example (Fig. 4). The evolutionary pressures must have been strong, as similarities to their supposed nearest relatives, the cryptobranchids, are few.

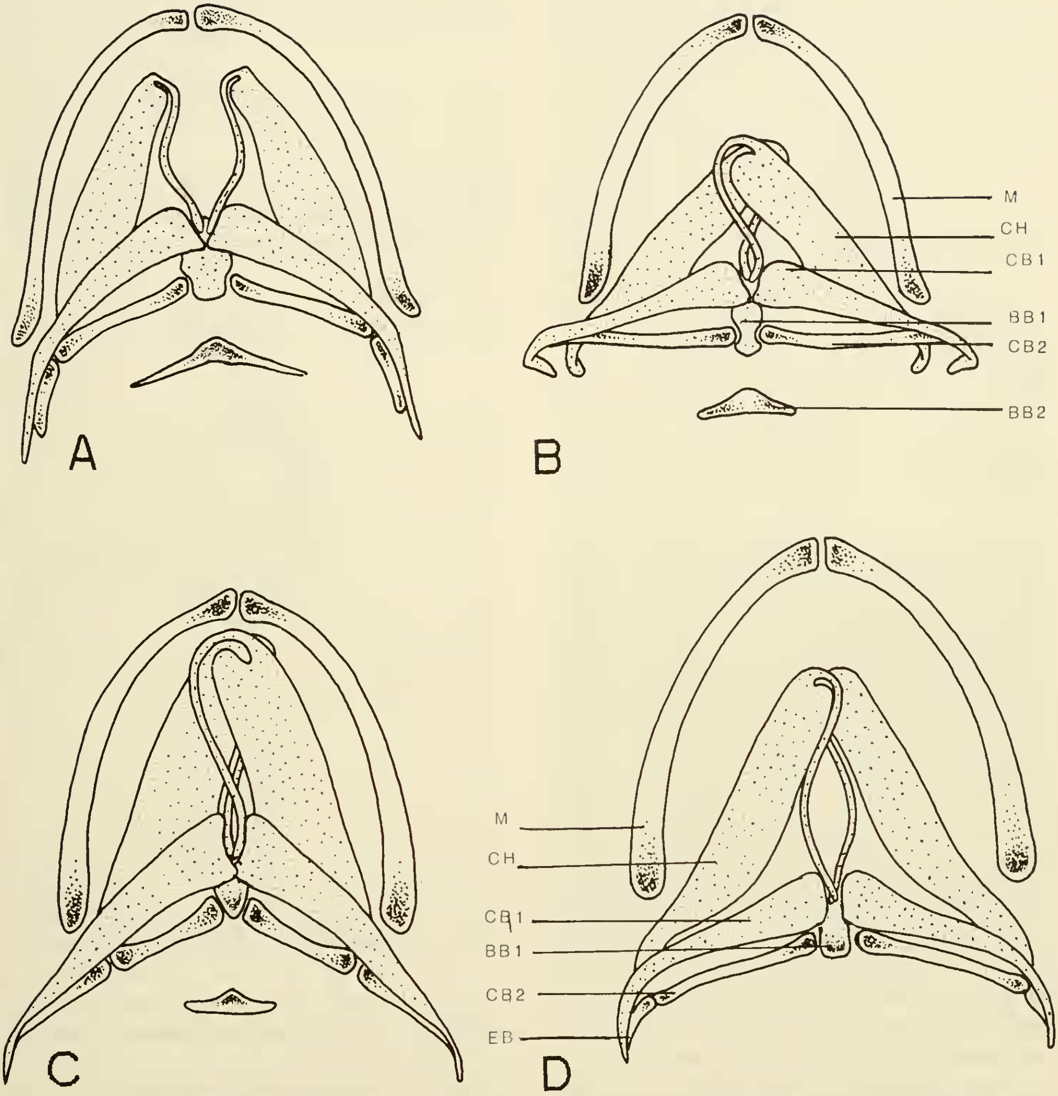

Fig. 4. Ventral view of the hyobranchial apparatus of: A, *Ranodon sibericus;* B, *Hynobius keyserlingii;* C, *Hynobius naevius;* and D, *Hynobius tsuensis.* M = lower jaw; CH = ceratohyal; CB1 = ceratobranchial #1; BB1 = basibranchial #1; CB2 = ceratobranchial #2; BB2 = basibranchial #2; EB = epibranchial.

The hynobiid salamanders possess the following structures as part of the hyobranchial apparatus: first and second basibranchial, ceratohyal, ceratobranchial, and epibranchial. The first basibranchial is small and rodlike, with small anterolateral cornua (Fig. 5). The first and second ceratobranchials attach solidly to the first basibranchial. There does not appear to be any direct attachment with the ceratohyals. The basihyals and the hypohyals are missing or perhaps fused with the ceratohyals. The ceratohyals are broad, flat, and thin cartilages that lie lateral and anterior to other parts of the hyobranchial apparatus. The anterior end of the ceratohyal is located near the symphysis of the lower jaw. A curious extension of the lateral edge of the ceratohyal is drawn out into a small rod that loops over the anterior end of the cartilage and continues posteriorly along the medial line, ending in

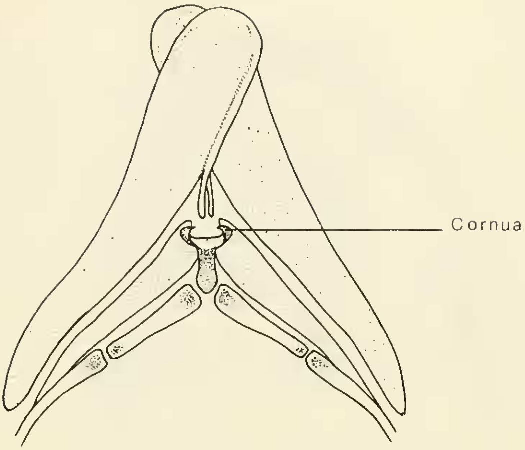

Fig. 5. Dorsal view of the hyobranchial apparatus of *Hynobius naevius*.

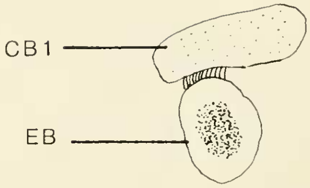

Fig. 6. Cross section of the distal ends of the ceratobranchial and epibranchial as observed in Hynobiidae. CB1 = ceratobranchial #1; EB = epibranchial.

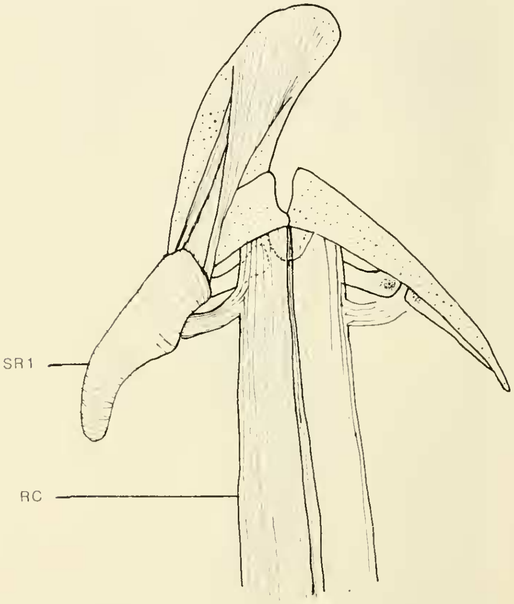

Fig. 7. Musculature of the ceratobranchial complex. SR1 = Subarcualis rectus 1; RC = Rectus cervicis.

connective tissue and bound with its partner, just dorsal to and at the anterior end of the basibranchial (Fig. 5). The first ceratobranchial is also flattened and relatively large, with its anterior end located at the level of the anterior end of the basibranchial and connected to its ventral surface. The ceratobranchial is found ventral to and overlapping the posterior half of the ceratohyal. The posterior portion of the second ceratobranchial and its epibranchial are closely adherent to a flattened distal surface of the first ceratobranchial. These are tightly bound together by connective tissue and muscle fibers (Figs. 6, 7). We did not find an epibranchial on the first ceratobranchial. The second ceratobranchial is small and rodlike. It is attached at its anterior end to the posterior end of the first basibranchial and extends posterolaterally, to be partially encased with the first ceratobranchial. The unity of the first and second ceratobranchials is further evidenced by the presence of the subarcualis rectus 1 muscle. This muscle originates on the anterior ventral surface of the ceratohyal and extends posteriorly to wrap and encase the lateral ends of the first and second ceratobranchials (Fig. 7). A slip of the rectus cervicis muscle also extends laterally to become incorporated into this same structure. This same muscle arrangement also occurs in primitive plethodontid salamanders and operates the functions of the tongue. In the more advanced plethodontid salamanders the tongue is free and the subarcualis rectus 1, by its contraction, is able to extend the tongue a great distance out of the mouth in order to capture prey. The more primitive plethodontids, lacking the free tongue, are closer to the condition observed in the hynobiids. Dunn (1923) referred to the hynobiid tongue as being "sessile, but free at the lateral and posterior edges." The argument by Regal (1966) that there is a relationship between the feeding patterns (and perhaps a relationship in the anatomical structures associated with feeding) of Ambystomatidae, Plethodontidae, and Hynobiidae may warrant more consideration than it has received.

Three of the four species dissected possess a second basibranchial (os thyroidum) (Figs. 4A,B,C), a small triangular bone found posterior to the other structures of the hyobranchial apparatus. This small bone is connected to the hyobranchial apparatus by connective tissue and muscle fibers. It was not found in *H. tsuensis*.

The dissections of the four species of the family Hynobiidae demonstrate a remarkably uniform consistency in the structures of the hyobranchial apparatus. This is especially true when we consider that the family has undergone an adaptive radiation that has resulted in systematists dividing the family into nine genera (Duellman and Trueb 1986). There is also remarkable variation between hynobiid throat structures and those of other families.

Two characters appear to be unique to the family Hynobiidae. The anterior end of the ceratohyl thins into a slender rod of cartilage that extends mesally and ventrally to approach or contact the anterior end of the first basibranchial. The posterior ends of the ceratobranchial rods are encased in connective tissue and are not solidly attached to the basibranchial; thus, it appears that considerable flexibility of movement occurs. This latter may be ascertained from the position of these structures as drawn from the preserved specimens.

The distal third of the first ceratobranchial has a flattened surface on its mesal side onto which the posterior part of the second ceratobranchial and its epibranchial are tightly enclosed by connective and muscle tissues (Fig. 6). This may provide greater support in the center of the throat area. This structure is reminiscent of the M. subarcualis rectus that occurs in some plethodontids, the genus *Pseudoeurycea*, as an example (Tanner 1952). The presence of the second basibranchial in essentially the same location as in primitive plethodons is also suggestive of an ancestral relationship.

The Cryptobranchidae demonstrate significant structural variation within the family. It appears that *Andrias davidianus* is the most advanced, that is, when compared with the Japanese and American species (Figs. 1–3). The throat structures of the genus *Cryptobranchus* indicate a semilarval condition not found in the oriental species. A transition of the hyobranchial apparatus from *Cryptobranchus* through *M. japonicus* to *A. davidianus* is evident in the consolidation of the skeletal elements to form in the latter (*davidianus*) structures that are closely adhering to each other in contrast to the looseness observed in *Cryptobranchus*. The strengthening of these structures may not be just the completing of metamorphosis to full adults; perhaps the increase in the size of adults demanded greater support in the hyobranchial apparatus.

In 1837 Tschudi described the genus *Megalobatrachus* and included in it the giant salamanders of Japan. Because of its size and similar external characteristics, it has been retained by most authors in the genus *Andrias*. After examining the anatomy of various families, and particularly the cryptobranchid *japonicus*, Hilton (1946, 1947) retained the giant salamanders of Japan in the genus *Megalobatrachus*. A comparison of the skeletal structures of the throat shows a consolidation in *davidianus* not seen in *japonicus*. Furthermore, in *davidianus* the first basibranchial is missing and the second has been enlarged to give greater support to associated structures. Based only on the hyobranchial apparatus, the differences are substantial enough to justify the retention of three genera in the family Cryptobranchidae: *Cryptobranchus*—American hellbender, *Megalobatrachus*—giant salamander of Japan, and *Andrias*—giant salamander of China.

Retaining these families (Cryptobranchidae and Hynobiidae) in the same order (Cryptobranchoidea) may be justified based on the primitive characters indicated above of external fertilization and retention of the angular bone in the lower jaw. There are, however, few similarities in the throat anatomy that would indicate a close relationship. Furthermore, the external anatomy does not indicate a close relationship. Both oriental cryptobranchid species are much larger than any of the hynobiids and exhibit an aquatic habitus not as apparent in hynobiids. The fact that hynobiids have diversified as they radiated into various habitats suggests that they have retained a biological vitality not present in the oriental cryptobranchids.

We have been privileged to examine only one specimen of each of the oriental species. There are few oriental cryptobranchid specimens in U.S. collections and these not available for dissection. Therefore, only one side of the throat area was dissected and this to determine only the position of the skeletal parts. A

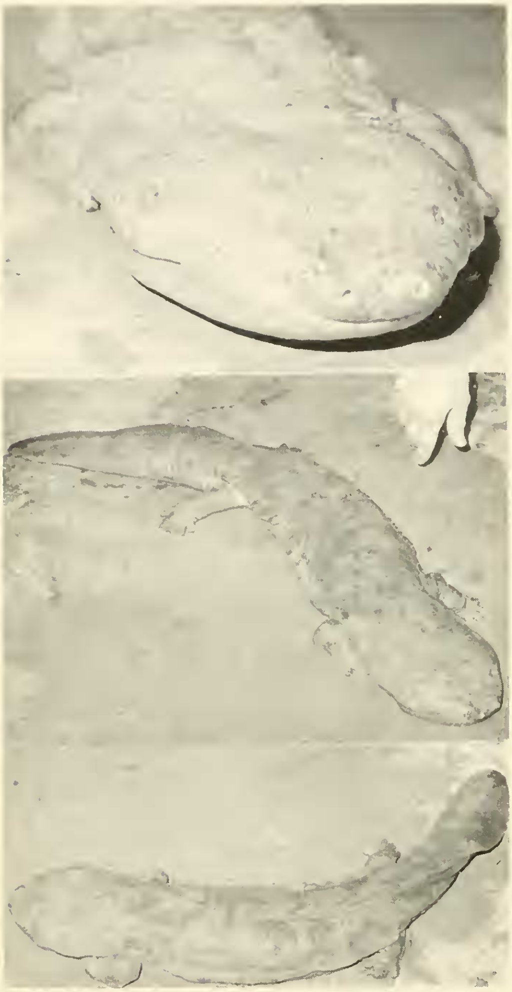

Fig. 8. Photographs of *Andrias davidianus* provided by Dr. James Kezer.

complete examination of the soft tissue and skull may demonstrate additional character variations.

As we examined the three species of the family Cryptobranchidae, we felt a constant impression that we had before us perhaps the most primitive representatives of the salamanders, if not of all Amphibia. The photographs of *A. davidianus* (Fig. 8) indicate little external specialization, with the exception of added skin folds on the body and tail. Aside from the hyobranchial apparatus of the cryptobranchids, which is unspecialized when compared with other families including the hynobiids, those characters listed by Dunn (1926), Morescalchi et al. (1977), and Sessions et al. (1982) provide further evidence that they are an archaic group. Some confirmation of this is also found in the wide distribution in much of the northern hemisphere. Fossil records indicate that the cryptobranchids were extant early in the Cenozoic and appear to have had their origin in late Cretaceous. One might speculate that in those turbulent geological times survival demanded a return to or a retention of a stream habitat, where they have remained to the present with little change. Therefore, one group, *C. alleganiensis*, with its gill bars, has persisted as semilarvae, whereas the asiatic species have evolved to full adults and have increased in size. The fossil record is as yet incomplete and does not provide enough evidence to determine the status of the ancestral stock. The hyobranchial apparatus of *C. alleganiensis* with its retained gill bars does suggest that this species may be similar to the primitive stock. At least it inhabits an area that is geologically old enough to have permitted a long existence in a region affected by relatively little habitat change since late Cretaceous or early Tertiary. If this is true, then the absence of gill bars is a derived character in the Asiatic species.

We find the family Hynobiidae to be a specialized group when compared with the cryptobranchids. We consider the specialized hyobranchial apparatus to be inconsistent with what one would expect from a group having such primitive characters as those indicated above. Using only the data from the hyobranchial apparatus, we find it difficult, in spite of obvious primitive characters, to see a close relationship to the cryptobranchids.

Dunn (1923) states that the

> hyobranchial apparatus of the family (Hynobiidae) agrees with that of the Cryptobranchidae in having the ceratobranchial and epibranchial of the first arch fused into a cartilaginous rod, and in having the ceratobranchial and epibranchial of the second arch present and free.

This generalized statement is far from detailing the specializations in hynobiids as compared with the generalized loose association of the skeletal structures in cryptobranchids. Were we to base conclusions on data obtained from the hyobranchial apparatus of the two families, we would find it more difficult than did Dunn (1923) and others to endorse the idea of a close relationship between them. The slender cartilaginous rod extending from the anterior end of the ceratohyal is unique to hynobiids, as also are the presence of an os thyrodeum and the closeness of the distal ends of the ceratobranchials (Fig. 4); these are not present in the cryptobranchids.

The two families included in the superfamily Cryptobranchoidea (Dunn 1923) both have primitive characters not found in other salamander families, characters that indicate their having descended from a common ancestor. The hyobranchial apparatus does not appear to provide this same relationship. There is good reason to believe that there were several lines of primitive stock in late Cretaceous and/or early Tertiary giving rise to present-day families, with only two retaining some characters that may have been present in several of the ancestral stocks. We find it difficult, based on the hyobranchial data, to see a close relationship. Retaining the Cryptobranchidae and Hynobiidae together in a single superfamily is perhaps more systematic convenience than phylogenetic fact.

Acknowledgments

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